Contrasting Space and Food Use Among Three Species of Juvenile Pacific Salmon (*Oncorhynchus*) Cohabiting Tidal Marsh Channels of a Large Estuary

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CONTRASTING SPACE AND FOOD USE AMONG THREE SPECIES OF JUVENILE PACIFIC SALMON (*ONCORHYNCHUS*) COHABITING TIDAL MARSH CHANNELS OF A LARGE ESTUARY

by

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ABSTRACT

Age 0 juvenile chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), and pink salmon (*O. gorbuscha*), occupy tidal channels of inner estuarine marsh habitat of the Fraser River for up to several months of their spring seaward migration, although pink only during even-numbered years. We investigated the spatial and temporal habitat use and dietary overlap of these species from February to June during 1986, 1988 and 1989. Peak occurrence of pink and chum in trap net catches occurred during March to early May, whereas chinook salmon juveniles dominated catches in late May and June. Spatial distribution within tidal channels was species-specific. Mid-channel trawl catches of all three species were significantly lower near the bottom than near the surface. Most pink salmon were caught near surface in the center of channels, whereas chum and chinook were most abundant within 1.5 m of the channel banks. Diet of the three species differentially included elements of the benthic, planktonic, and surface prey present. Diet overlap by prey volume (Schoener Index) was highest between chinook and chum salmon (90%), and low between pink and the other two species (chum 32%, chinook 30%). Spatial, temporal, and diet overlap among the cohabiting species suggested segregation of resource use during their estuarine residency period.

RÉSUMÉ

Les jeunes d'âge 0 du saumon quinnat (*Oncorhynchus tshawytscha*), du saumon kéta (*O. keta*) et du saumon rose (*O. gorbuscha*) occupent les chenaux de marée de l'habitat marécageux de l'intérieur de l'estuaire du Fraser pendant plusieurs mois durant leur migration printanière vers la mer. Le saumon rose n'est toutefois présent dans ces chenaux que lors des années paires. Nous avons étudié les chevauchements spatio-temporels de ces espèces sur le plan de l'utilisation de l'habitat et de l'alimentation de février à juin en 1986, 1988 et 1989. Les prises de saumon rose et de saumon kéta dans les parcs en filet ont été les plus nombreuses de mars au début du mois de mai, tandis que les saumons quinnats juvéniles ont dominé les prises à la fin du mois de mai et en juin. La répartition spatiale à l'intérieur des chenaux de marée variait selon l'espèce. Les prises des trois espèces au chalut dans le milieu des chenaux étaient beaucoup moindres près du fond que près de la surface. La plupart des saumons roses ont été capturés près de la surface dans le centre des chenaux, tandis que le saumon kéta et le saumon quinnat étaient les plus abondants à moins de 1,5 m des rives des

chenaux. Le régime alimentaire des trois espèces consistait en divers organismes benthiques, planctoniques et de surface. Le chevauchement des régimes alimentaires sur le plan du volume des proies (indice de Schoener) était le plus élevé entre le saumon quinnat et le saumon kéta (90 %) et le plus faible entre le saumon rose et les deux autres espèces (saumon kéta 32 % et saumon quinnat 30 %). Les chevauchements spatio-temporels et alimentaires entre les trois espèces suggèrent un isolement sur le plan de l'utilisation des ressources durant leur période de résidence en milieu estuarien.

INTRODUCTION

Young of three Pacific salmon species spend varying amounts of time residing in the tidal marsh channels of the inner Fraser River estuary, British Columbia during their downstream migration (Levy and Northcote 1982). The duration of their residency depends upon species and lasts a few days (pink salmon - *Oncorhynchus gorbuscha*), nearly two weeks (chum salmon - *O. keta*), or up to a month (chinook salmon – *O. tshawytscha*). Although the general features of their distribution and feeding in this part of the estuary have been studied (Levy and Northcote 1982), microspatial and temporal distribution, as they influence the use of available prey, have not been examined.

Many Pacific coast estuaries have been degraded in the last century as a result of poor land-use practices. For example, agricultural dyking, industrial development and urbanization have resulted in the loss of much of the tidal marsh habitat of the Fraser River estuary, near Vancouver, British Columbia (Levings 1985). Although some limited success toward restoration of such habitat has been made (Levings and Nishimura 1996), serious declines in many salmon stocks of the Fraser River watershed continue (Slaney et al. 1996, Northcote and Atagi 1997).

Tidal marshes are broadly distributed along the outer front of the Fraser River estuary. However, it is the inner marsh habitat - now for the most part restricted to the Woodward Island complex and Ladner Marsh in the Main Arm of the Fraser River - that is heavily used by young of pink, chum, and chinook salmon (Levy and Northcote 1982). With young of these three species co-occurring in the tidal channels of such marsh habitat at least temporarily, the potential exists for differential use of space and food resources.

In this study, we investigated the differential occurrence in time and space, and the contrasting use of available prey resources, among age 0 juvenile pink, chum, and chinook salmon, during the estuarine residency portion of their seaward migration. We first determined the temporal and spatial patterns of tidal channel habitat use by each species. We then examined the abundance of invertebrate prey and contrasted prey consumption by each of the three species.

METHODS

We selected three tidal channels (Fig. 1; Table 1) in two locations of the most extensive and complex tidal channel network of the main arm of the Fraser River for study in 1986-89. These were third order channels, averaging 9-10 m wide and up to 2 m deep at high tide throughout much of their length. At low tide, these channels almost completely de-watered; before overtopping at high tide, they had lengths of 276-300 m from the sampling site to the upper point used by juvenile salmon. Sites had not appreciably changed in the decade between the (Levy and Northcote 1982) study and our investigation.

We sampled juvenile salmon using two types of nets – a trap net and a trawl net. Trap nets were used to capture and enumerate juvenile salmon in entire tidal channels (~1000's m^3). Trap nets were of 0.6 cm mesh, 2.4 m high and set across the entire mouth of tidal channels when deployed. We used them to sample juvenile salmonids in the three tidal channels. We tied trap nets onto the same permanent station posts described by (Levy and Northcote 1982), at high tide. These were fished until the channels had de-watered during the ebb tide, capturing most of the fish in the tidal channels. Fish previously entering tidal channels during the flood tide, were retained in the trap bag, which remained in enough water to allow for survival of fish during sampling and enumeration (see (Levy and Northcote 1982) for a full description of our trap nets and study sites).

We used the trawl to sample fish in small discrete volumes (15 m^3) to determine the spatial distribution of juvenile salmon with respect to tidal channel microhabitats. The trawl was 1.5 m wide and 0.5 m high and was divided into two separate tapering cod-end bags of 0.3 mm nylon mesh, each fishing half the net opening. The header support of the trawl was fitted with floats to support the trawl for edge and centre channel surface tows; a weighted bar was attached onto the footer support for near-bottom tows. The trawl was pulled for replicated 20 m lengths along tidal channel edges, as well as for centre channel 20 m lengths along the surface and near-bottom, by two ropes (one on the opposite edge of the tidal channel to avoid disturbance near its mouth).

The lower mainstem Fraser River at New Westminster (30 km upstream from its mouth) has a mean annual discharge of 3600 m$^3 \cdot$s^{-1} (Northcote and Larkin 1989); minimum daily flows occur in February with maximum flows in June during the years of our study. Mean monthly discharge in 1986 (Fig. 2a) was slightly higher for most months between February and June, than for other years in the 1985-89 period.

We measured water temperature, salinity and conductivity using a YSI Model 33 conductivity meter, and water transparency using a 20 cm diameter Secchi disc. We determined turbidity of field samples in the laboratory using a Fisher Model DRT 100 turbidimeter. Mainstem mean monthly temperature in February was 3-4 °C, which rose to 13°C in June; maximum temperatures reached 18°C in August. Tidal channel water temperatures (Fig. 2b) were slightly lower than the mainstem river mean in February, but slightly higher in June.

Transparency in Ladner Marsh D4 tidal channel was highest in February (>75 cm Secchi depth) and decreased to about 50 cm from March to May with a low near 25 cm in June (Fig. 2c). Transparency in the Woodward Island tidal channel was nearly twice that in Ladner Marsh from February to early April but decreased sharply after mid-April to values lower than Ladner Marsh in May, being more dominated then by low transparency Main Arm water.

Turbidity in Ladner Marsh tidal channels was low from February through early April, but increased after mid-April to a peak in mid-May and declined throughout

June (Fig. 2d). Water clarity was higher in the Fraser Main Arm than in Ladner Marsh in late February to early March. However, clarity declined rapidly during the May to early June freshet in both locations.

Surface water salinity in Ladner Marsh tidal channels (Fig. 2e) was about 6‰ in mid-February, falling to spring-early summer lows <1‰ during the late April to June period, coincident with spring freshet. Bottom water salinity was up to twice surface values in the tidal channels from March to early May, but not thereafter. Conductivity values tracked those for salinity throughout the study period (Fig. 2f).

Benthic and epibenthic macroinvertebrates in the upper 5 cm of mud bottom were sampled at approximately two week intervals throughout the sampling period, using a 4.7cm diameter core sampler, and preserved with 10% formalin in the field. During each interval, 2-3 (1986) or 5 (1988) samples were taken. In the laboratory, entire replicate samples were, first washed through a 300 μm mesh screen to remove the larger organisms. One quarter of the sample passing through this screen was then passed through a 158 μm screen. Macroinvertebrates retained by the screens were removed and identified under a dissecting microscope, multiplying counts from the fine-meshed portion by four, then multiplying all counts by 5.76 to express them as density per 100 cm^2.

Planktonic macroinvertebrates were sampled at approximately two week intervals throughout the sampling period, using a suction pump drawing 35 l min^{-1} for 2 min, into a 70 μm net and bucket. Two to four replicate samples were taken close to the D4 station at high tide from near surface to 1.5 m depths and preserved in 4% sugared formalin. Total counts of eight different taxa were made with a dissecting microscope (at 10–50x magnification).

Surface drifting macroinvertebrates were temporally sporadic, depending on the interplay of wind and tidal action at the tidal channel edge. However, juvenile salmon could be seen feeding intensively on this surface drift when it was available in a given area. We sampled drifting insects and other potential invertebrate prey with fine meshed aquarium nets, surface-hauled plankton nets, and other gear. These collections were opportunistic in nature and therefore, not quantifiable.

We determined prey consumed by juvenile salmon by analysis of stomach contents of fish captured during the seasonal trap net series. The stomachs (lower esophagus to the pyloric sphincter) of the salmon digestive tracts were dissected out and the contents sorted in a Petri dish under a dissecting microscope. Total counts were made for each prey taxon and volumes estimated by liquid displacement in a volumetric tube.

Our trawl data exhibited a non-normal error structure. Therefore, statistical analysis could not be conducted using standard parametric techniques. We determined significance by calculating the probability of generating the observed or more significant results by chance among compared habitats from

500 bootstrap estimates of the mean densities observed (as described in Manly 1991). We used Schoener's Index (Schoener 1982) to compare the overlap in diet among the three cohabiting salmon species. All other statistical procedures used by us are commonly utilized in ecological investigations (e.g., ANOVA, Student's t-test, Kruskal Wallis, Mann Whitney U tests). We used a critical value of p=0.05 for all tests of statistical significance.

RESULTS

JUVENILE SALMON ABUNDANCE

The juveniles of three species of salmon followed a similar pattern of seasonal percent abundance in Ladner Marsh and Woodward Island tidal channels (Fig. 3). Pink salmon had a short period of moderately low abundance in the tidal channels from March to May. Chum salmon reached maximum abundance in tidal channels near mid-March, well before sizable numbers of chinook salmon appeared in April. Relative abundance of chinook juveniles increased through May into June (Fig. 3).

Juvenile salmon density in the tidal channels of Ladner Marsh was estimated by multiplying trap net catches by gear efficiency factors for the three species - 2.22 for chum, 2.05 for pink, and 1.61 for chinook - relevant to our gear, study sites, and species (Levy et al. 1979). Corrected trap net catches were divided by tidal-channel area upstream of the trap nets, which was available for use by juveniles (Table 1). Juvenile chum density in tidal channels was higher than that for pink or chinook salmon throughout most of the spring (Fig. 4). In late May and in June, density of all three species declined; however, chinook density exceeded that of pink and chum.

JUVENILE SALMON DISTRIBUTION WITHIN TIDAL CHANNELS

There were significant differences in mean density and distribution of the three species between edge and centre regions of Ladner Marsh tidal channel D1 (Table 2). Over twice as many pink juveniles were taken in trawl net surface tows at the centre of the tidal channel than at the edge. The reverse was the case for chum (10:1 edge vs centre surface) and chinook (nearly 2:1 edge vs centre surface), with the difference being statistically significant for chinook - ANOVA, p=0.024. Pink and chum were never taken in the middle of the channel near the bottom. Chinook were caught near the bottom in low densities compared with the centre surface and channel edge; chinook density in each location was higher than other species (Table 2). Mean density of chinook in the shoreward half of the trawls (i.e. inner half of the net) was over twice that taken in the channel half (i.e. outer half of the net) - 1.30 versus 0.60 per 15 m^3. However, data were too few to establish if this difference was statistically significant in our study. Densities of pink and chum juveniles taken at the inner and outer edge compartments of the trawl net were also too low to make similar comparisons.

JUVENILE SALMON SIZE

Pink salmon were the smallest of the three species of juvenile salmon cohabiting in the Ladner Marsh tidal channels - none exceeding 36 mm Fork Length (FL) (mean 33.3mm, Table 3). Chum salmon were somewhat larger – attaining 43 mm FL (mean 38.9mm). Chinook were the largest of the three species - some exceeding 60 mm FL (mean 43.5 mm). There was no appreciable seasonal change in size of pink or chum juveniles, except for chum in early June. In contrast, mean length of chinook increased after mid-May, reaching sizes of 55-80 mm FL depending on location and year (Table 3).

EPIBENTHIC PREY

Nine different taxa were common in the epibenthic samples taken from tidal channels (Fig. 5). Total numbers averaged close to 1000 macroinvertebrates per 100 cm^{-2} for early April, May and June 1986, but over four times higher in late April (Fig. 5). Total numbers in 1989 were almost four times higher than those in 1986. Harpacticoid copepods were the most abundant epibenthic taxon, followed by nematodes, ostracods and oligochaetes. Two amphipod species were common, *Corophium spinicorne* and *Anisogammarus conferviculus*, with the former being by far the most common. Isopods (mainly *Gnorimosphaeroma oregonensis)* were also present. Chironomid larvae and polychaete worms were relatively low in abundance but present at all sampling periods. Leeches, water mites, clams and gastropods occurred only infrequently.

PLANKTONIC PREY

Seven planktonic taxonomic groups were regularly taken by pump sampling within the upper 1.5 m at high tide in the D4 Ladner Marsh tidal channel (Fig. 6). Total abundance of planktonic invertebrates was highest in April and May with numbers close to 10 l^{-1}. Similar to epibenthic invertebrates, planktonic forms were dominated numerically by harpacticoid copepods, with numbers close to 6 l^{-1} during April and May. Copepodite stages of copepod species were the next most abundant group, followed by ostracods, nematodes and oligochaetes which we combined, as they likely represented temporarily "planktonic" individuals due to the ebbing tide. Cyclopoid and calanoid adults, as well as two cladoceran taxa - *Daphnia* and *Bosmina* - were in low abundance throughout the study period (Fig. 6).

Copepod nauplii were the most abundant group (densities ranged up to 150 l^{-1} between March and June). Nauplii were never taken as prey by juvenile salmon; therefore we have not shown them. Insect larvae, water mites and very small fish larvae were only rarely recorded.

SURFACE DRIFT PREY

Qualitatively, surface macroinvertebrate drift was highly variable, due to wind and tidal influences. We were only able to make qualitative statements about macroinvertebrate drift abundance. Juvenile salmon periodically could be seen feeding intensively on this surface drift. Drifting macroinvertebrates consisted mainly of adult aquatic insects, especially chironomids and to a lesser extent other non-aquatic insects associated with riparian vegetation.

JUVENILE SALMON DIET

Over the spring period when the three species of salmon were present together in the Ladner Marsh tidal channels, there were major differences in both the prey frequency distributions and mean stomach fullness index (Fig. 7). Pink had the lowest and chinook had the highest mean gut fullness; chum was intermediate. A Kruskal-Wallis test on fullness indices was significant ($p < 0.0001$), as were Mann-Whitney tests between pink and chum ($p = 0.0167$), pink and chinook ($p < 0.0001$), and chum and chinook ($p = 0.0030$). The difference between stomach fullness of chinook captured on the flood and ebb tide was not significant (Mann-Whitney U test $p = 0.2548$). We did not capture sufficient individuals to permit similar tidal comparisons for pink and chum salmon.

Nine different prey taxa groupings were regularly consumed by cohabiting pink, chum and chinook juveniles in the Ladner Marsh tidal channels (Fig. 8), and these were assigned to three different probable capture locations - epibenthic (five taxa), midwater (two taxa), and surface (two taxa). Pink juveniles fed on mainly one taxon of epibenthic prey - harpacticoid copepods - whether measured by frequency of occurrence, numbers or volume (Fig.8). Chum and chinook consumed all nine prey taxa, taking large quantities of epibenthic prey - including some Neomysis mercedis - and adult surface insects. There were no significant differences in percent number or percent volume of adult insects consumed by chinook juveniles between flood and ebb tide in the tidal channels.

We were able to make comparisons of major prey taxa between months (Table 4) for chinook salmon. Occurrence of harpacticoids in juvenile chinook stomachs was highest in early spring (March-April), but declined by late spring (May). They were absent from the diet by early summer (June). Amphipods and insect larvae were important in the diet early spring to early summer. Collembola were minor prey items throughout. However, consumption of other adult insects – mainly dipteran forms – were important prey in early spring, and increasingly so as the season progressed from late spring to early summer.

All three salmon species preyed upon harpactacoids, but pink far more so than chum, and chum more so than chinook (Fig. 5-8). Nematodes were seldom consumed by chum and chinook, and not at all by pink juveniles. Although relatively abundant, ostracods were seldom consumed by any species. Large and moderately abundant Corophium and Anisogammarus prey contributed

mainly to chum and chinook diets. Except for abundant harpacticoid prey, planktonic taxa were rarely taken by any of the three salmon species. The epibenthic *Neomysis* was a minor prey item for chum and chinook; we did not observe it in pink salmon stomachs.

Indices of diet overlap by pink salmon with both chum and chinook were low, whether measured by numbers or volumes (Table 5). Index values greater than 60 suggest significant dietary overlap (Schoener 1982, Davis and Todd 1998). For pink-chum, and for pink-chinook, dietary overlap ranged between 30 and 50. In contrast, values between chum and chinook salmon were about 75 and 90 for numbers and volumes respectively, suggesting a high degree of dietary overlap between these two species.

DISCUSSION

Survival of juvenile fish is in part a function of size-dependant processes. Small individuals are generally at greater risk to predators than larger conspecifics (Miller et al.1988; Sogard 1997). Survival will generally favor individuals growing quickly while minimizing their exposure to predators (Werner and Gilliam 1984). Growth, which is both a size- and density-dependant process, is lower when prey density is low or when density of similarly-sized conspecifics is high. Juvenile fish should exhibit strategies of resource use, which promote rapid growth beyond those sizes most vulnerable to predators (Miller et al. 1988).

Hundreds of millions of juvenile Pacific salmon migrate seaward in spring and summer (Northcote 1976) from the Fraser River alone, during which time many may take up an estuarine residency period of variable duration (Levy and Northcote 1982). Among the species we encountered in our study, pink salmon exhibited the shortest residency period - a few days – while chinook were resident the longest – up to 30 days. Juvenile pink salmon are present in abundance only in even-numbered years (Northcote 1976). The residency of chum salmon was intermediate, between pink and chinook – up to 11 days. Within species, residency period has been shown to be size-related with large individuals commonly emigrating seaward earlier than small ones (Healey 1979, 1982; Murphy et al. 1987). In the Fraser River, two dominant life history strategies are known among chinook salmon populations – ocean-type and stream-type. The first migrates seaward as under-yearlings at small body sizes following a short freshwater residency. In contrast, stream-type individuals migrate seaward as age 1 or older fish. Predictably, stream-type migrants in the Fraser River are substantially larger that their ocean-type counterparts (Gregory and Levings 1998) and do not generally occupy tidal channels in our experience. The chinook we observed in this study were all ocean-type.

During their period of residency in the estuary, young salmon can exhibit high daily growth rates (0.2-0.6 mm FL d^{-1} for chinook - Levy and Northcote 1982; Fisher and Pearcy 1989; Dauble et al. 1989). Attaining high growth rates has been shown to be a function of preferred prey availability (Werner and Gilliam

1984). Epibenthic prey (principally harpacticoid and cyclopoid copepods) associated with the detrital food web predominate the diet of the smaller individuals (Naiman and Sibert 1979). Terrestrial insects and then fish contribute an ever-increasing proportion as individuals grow (Macdonald et al. 1987; Murphy et al. 1987; Brodeur 1991; Healey 1991). Individuals from populations with access to large prey show higher growth rates, compared with individuals from populations with access only to small-bodied prey (Rondorf et al. 1990).

Juvenile salmonids co-occuring in estuaries show some degree of spatial segregation (Murphy et al. 1987; Dauble et al. 1989), and use prey types most available to them in these microhabitats (Macdonald et al. 1987; Shreffler et al. 1992). In large streams and rivers (>25 m width), microhabitat segregation may act to minimize potential competition, especially for residents of widely varying sizes (Levings 1982; Macdonald et al. 1987). However, smaller waterways may offer no clear distinction among microhabitats. In this study, we have shown that habitat - prey preferences are expressed at very small spatial scales (<5 m) in the estuarine tidal channels, which suggests strong interaction among the three salmonid species we studied (e.g. Beacham 1993). Depletion of the largest prey may force juvenile salmon to rely on smaller, less preferred prey (e.g. chinook in Columbia River reservoirs, Rondorf et al. 1990).

In the Fraser River inner estuary, migration timing, residency, and prey consumption pattern among juvenile pink, chum, and chinook salmon were consistent with a strategy to minimize species interactions. Species migrated seaward at different times or consumed different prey. In our study, pink salmon juveniles migrating downstream occupied the inner estuary at small sizes. Our length frequency data suggested that these individuals leave after a short residency period consistent with earlier results for our sites (Levy and Northcote 1982). When they co-occurred with chum salmon in our study, pink occupied the middle of the tidal channels. In contrast, chum salmon, which arrived in the estuary at a similar time in spring as pink salmon, tended to occupy channel margins and feed on larger prey. Microhabitat and prey segregation between these two species may be significant. (Beacham 1993) has shown that juvenile chum may retard the growth of pink salmon when densities of chum are high.

Based on their high diet overlap in our study (90%), species interaction appeared highest between chum and chinook juveniles. However, this may have been reduced by the temporal residency pattern exhibited by the two species. In our study, chum arrived in the estuary earlier in the spring than chinook, and their numbers declined soon after chinook took up residency. Young-of-the-year chinook salmon arrived in the estuary from upstream sources later in the spring at relatively larger sizes than did pink and chum salmon, and they stayed the longest. Despite consuming similar prey and generally occupying similar spatial locations in the spring, interactions among the three species appears to have been minimized by temporal phasing of estuarine residency and microhabitat segregation. The latter may have reduced potential competitive effects, which could be expected from the high degree of dietary overlap alone.

ACKNOWLEDGMENTS

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Table 1. Morphometric characteristics of Ladner Marsh (D1, D4) and Woodward Island (W1) tidal channels sampled in the Fraser River estuary[a].

Characteristics	D4	D1	W1
Mouth width (m)	11.5	13.0	17.0
Station width (m)	8.7	9.7	9.9
Distance to mouth (m)	90	9	192
Channel depth (m)	1.8	2.2	1.8
Total channel length (m)	376	770	495
Used channel length (m)[b]	~276	~220	~300
Refuge distance (m)[c]	217	13	219
Total channel area (m^2)	3893	2323	4608
Used channel area (m^2)	~2200	~1000	~4050

[a]see Levy and Northcote (1982) for other habitat details
[b]used during spring to early summer by age 0 salmon
[c]distance to the nearest sub-tidal non-dewatering refuge

Table 2. Mean density [per 15 m^3 ± S.E.] of juvenile salmon in Ladner Marsh tidal channel D1 determined by edge and centre (surface, near-bottom) 20 m trawl net tows 26 March- 23 May (pink, chum), 26 March-11 June (chinook), 1986. Number of tows in parentheses.

Species	Edge	Surface	Centre Bottom
Pink	0.073 [± 0.041]	0.182 [± 0.041]	0
	(41)	(44)	(32)
Chum	0.235 [± 0.104]	0.023 [± 0.023]	0
	(34)	(44)	(32)
Chinook	0.736 [± 0.164]	0.442 [± 0.219]	0.125 [± 0.064]
	(53)	(52)	(40)

Table 3. Size (mm FL) of juvenile pink, chum and chinook salmon sampled by trap net in the Fraser River inner estuary tidal channels (Ladner Marsh, Woodward Island) in 1978 (data from Levy et al. 1979) and Ladner Marsh, D1, D4 in 1986 (this study).

	1978				1986			
	21 March -24 May			23 June	16 March-24 May			10-11 June
	Pink	Chum	Chinook	Chinook	Pink	Chum	Chinook	Chinook
No.	512	600	519	100	25	30	136	40
Mean	33.1	36.7	43.6	67.0	33.3	38.7	42.4	46.6
Range	27-37	30-57	35-63	51-82	30-36	33-43	32-62	34-54

Table 4. Monthly (March-June) changes in mean percent frequency, number and volume of major[a] prey taxa for juvenile chinook salmon in tidal channels of Ladner Marsh 1986. Sample size in parentheses.

Taxa	26 March - 29 April (41)			8 - 25 May (86)			10 - 11 June (34)		
	Freq.	No.	Vol.	Freq.	No.	Vol.	Freq.	No.	Vol.
Harpacticoids	26.8	25.0	13.7	9.3	8.9	5.5	0	0	0
Corophium[b]	26.8	9.5	13.5	7.0	3.0	4.2	29.4	14.8	16.2
Anisogammarus[c]	36.6	19.5	19.6	25.6	9.2	12.7	8.8	2.1	4.7
Insect larvae	22.0	8.2	9.2	32.6	17.2	12.5	29.4	20.8	18.2
Collembolids	14.6	3.5	1.2	18.6	8.1	5.5	11.8	7.5	7.1
Adult insects	56.1	29.8	34.1	69.8	41.4	48.5	61.8	44.2	43.5

[a] taxa shown where frequency of occurrence >10 for at least one monthly period
[b] *Corophium spinicorne*
[c] *Anisogammarus conferviculus*

Table 5. Overlap indices (Schoener 1982) for use of nine major prey taxa by age 0 pink, chum and chinook salmon co-occuring in Ladner Marsh tidal channels, March to May 1986.

Species pairs	Overlap indices	
	Prey numbers	Prey volumes
Pink versus chum	50.3	31.9
Pink versus chinook	32.6	30.1
Chum versus chinook	74.6	90.0

Figure 1. Ladner Marsh and Woodward Island study area in the Fraser River estuary, British Columbia (upper inset – Woodward Island; lower insets – Fraser River estuary from New Westminster to the Strait of Georgia and Fraser River location in southern British Columbia).

Figure 2. Water flow and site conditions in Ladner Marsh and Woodward Island, 1986-89, including comparisons with a previous study (Levy et al. 1979). A: Mean monthly (February to June) Fraser River mainstem discharge at New Westminster (1986) and B-F: water quality conditions at centre tidal channel near-surface. ● = Ladner Marsh D4 1986; O = Ladner Marsh D1 1989; × = Woodward Island W1, 1988; ⊙ = Fraser River Main Arm 1975; } = Main Arm 1979; Δ = Ladner Marsh D4 1979.
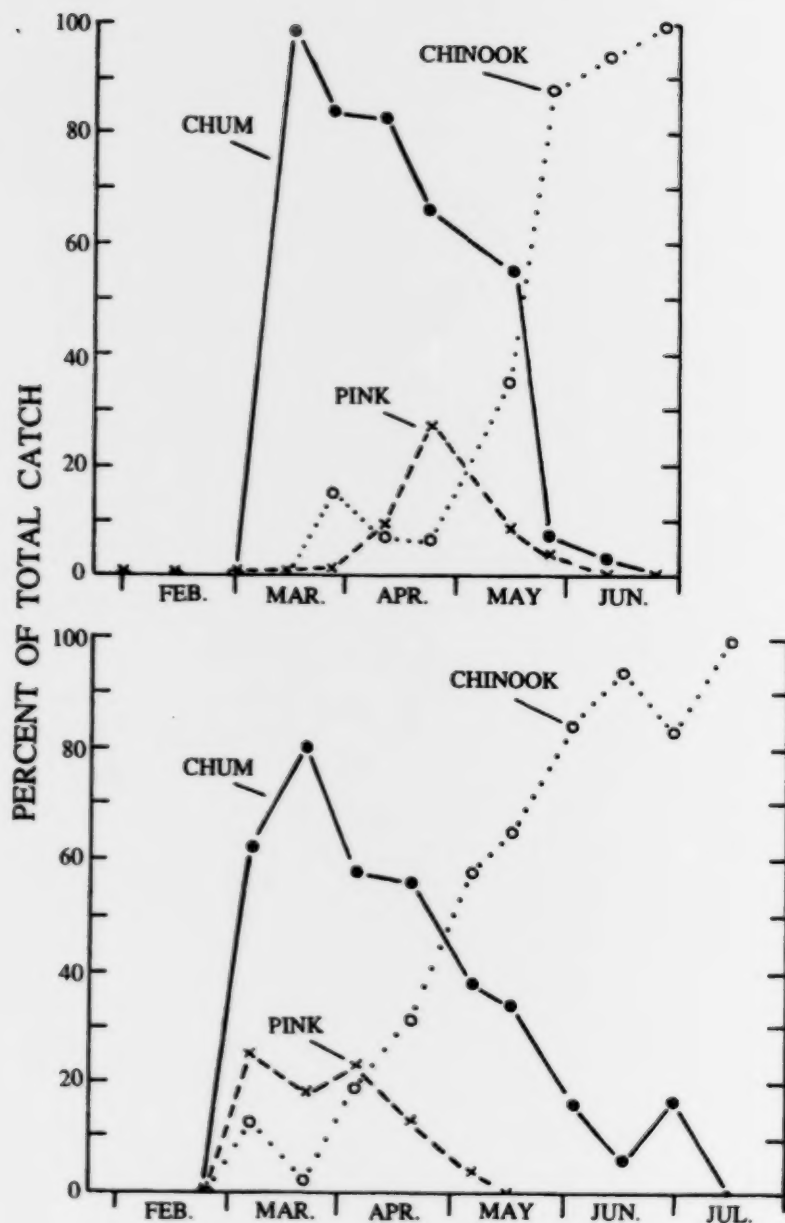
Figure 3. Percent contribution to total catch of juvenile pink, chum and chinook salmon by trap nets in tidal channels of inner marsh habitat of the Fraser River estuary (upper panel: Ladner Marsh sites D1, D4 mean for 1986; lower panel: Woodward Island site W1 for 1988).
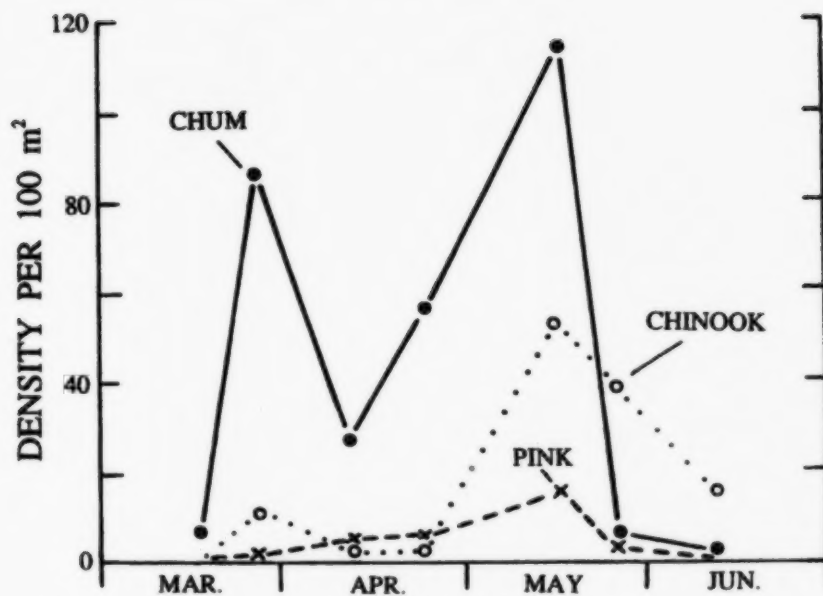
Figure 4. Seasonal change in density of juvenile pink, chum and chinook in Ladner Marsh tidal channel D1, 1986, estimated from trap net catches and tidal channel area used.
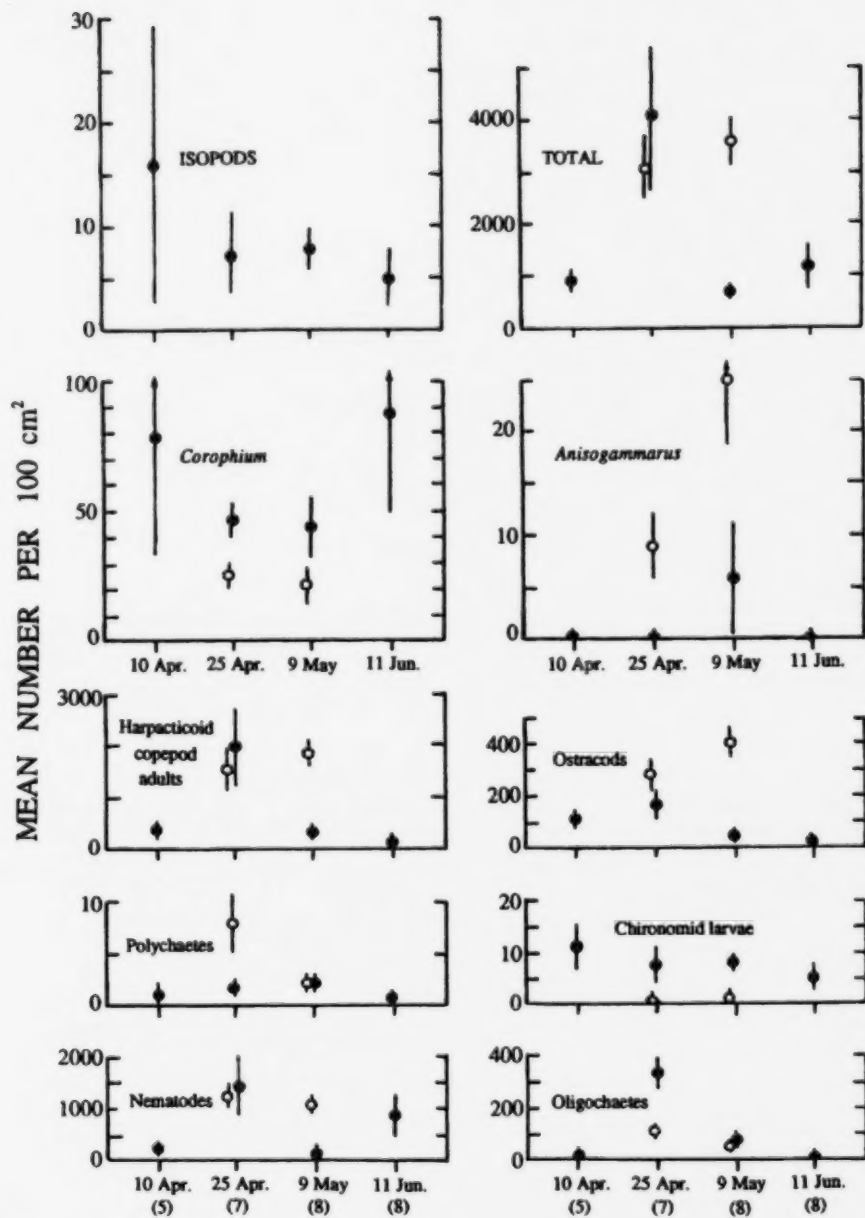
Figure 5. Mean monthly (spring to early summer) density of epibenthic
macroinvertebrates at Ladner Marsh tidal channel D4 in 1986 (●) and 1989 (O).
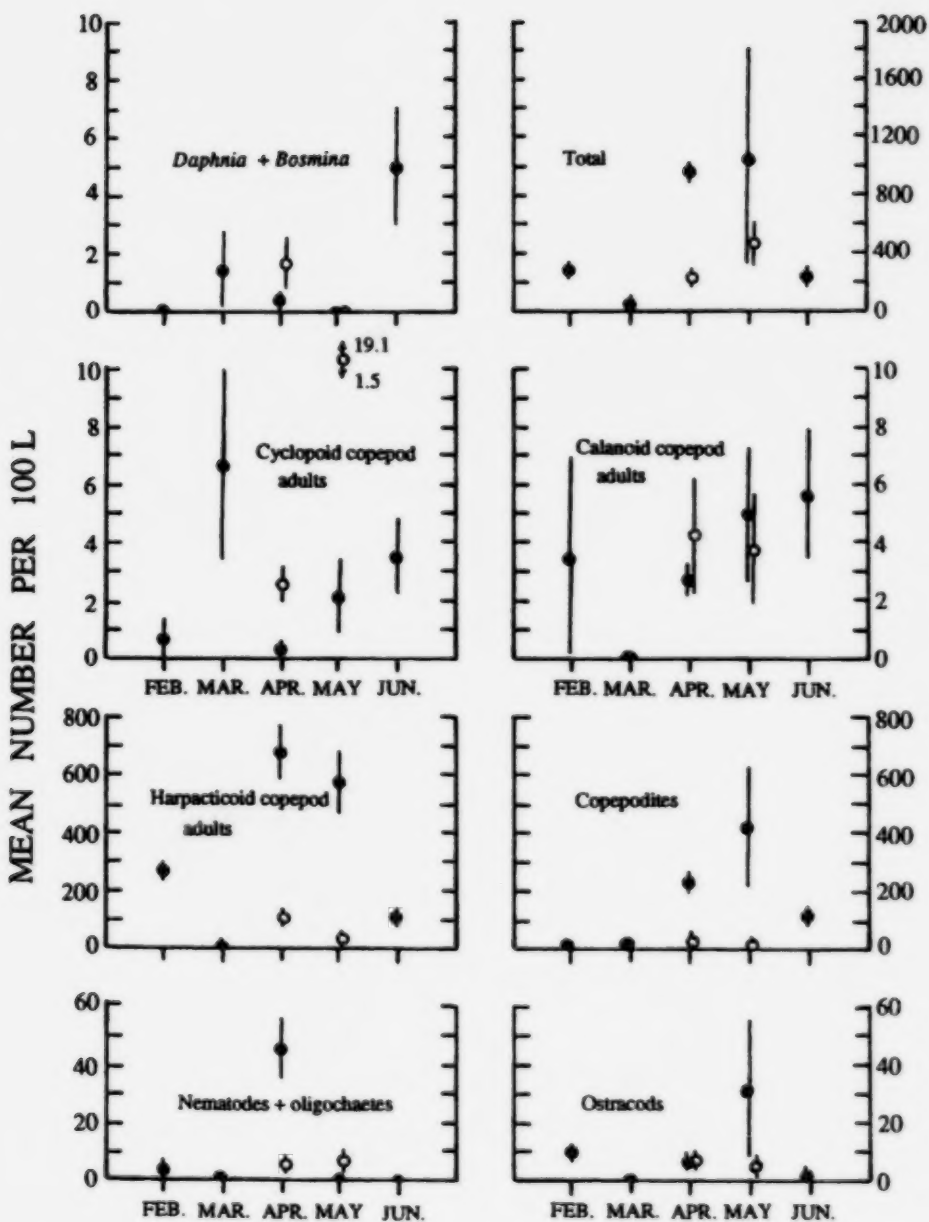Numbers in parentheses give sample sizes. Vertical lines represent standard error.

Figure 6. Mean spring to early summer density of planktonic macroinvertebrates at Ladner Marsh tidal channel D4 1986 (●) and 1989 (O). (vertical lines represent standard error).
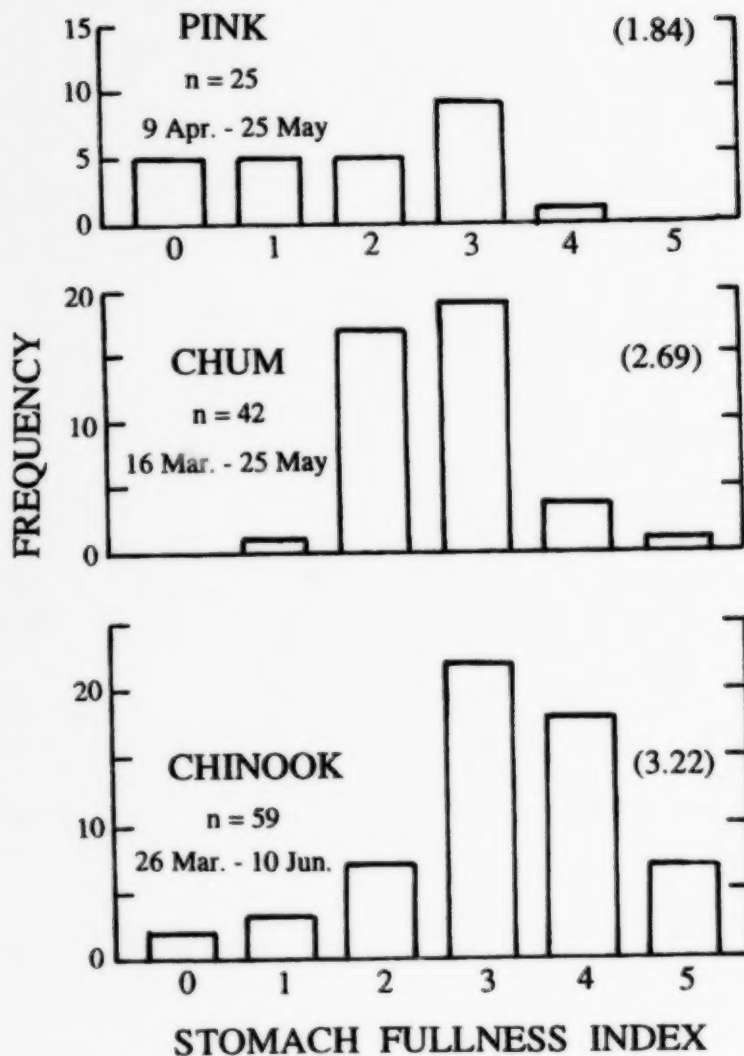
Figure 7. Frequency distributions of stomach fullness index (0 = empty to 5 = completely full) for juvenile pink, chum and chinook salmon captured by trap nets and cross-channel seining in tidal channels of Ladner Marsh 1986 (mean values in parentheses).
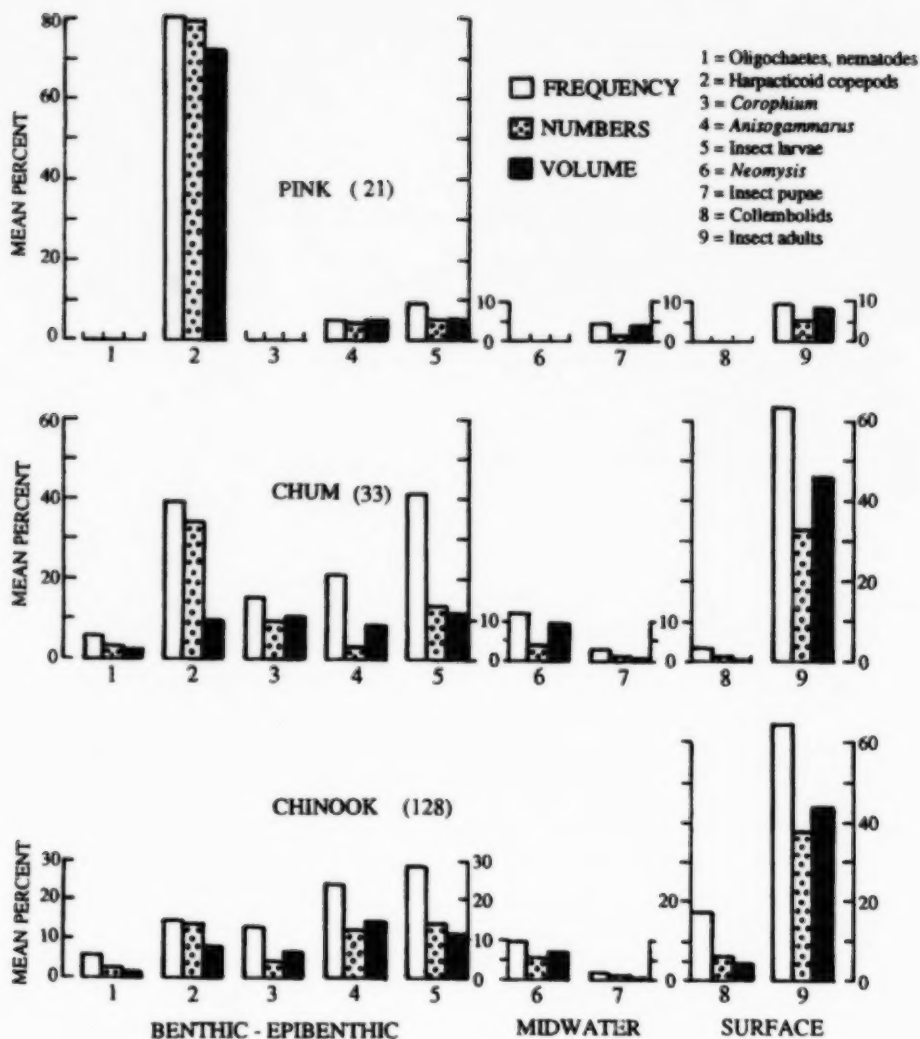
Figure 8. Comparative use of epibenthic, midwater (planktonic), and surface prey taxa taken by juvenile salmon during their period of cohabitation (March to May) in tidal channels of Ladner Marsh 1986 (harpacticoid copepods grouped with epibenthic taxa due to relative abundance – Fig. 5 and 6; number of fish in brackets).